VASCULAR EPIPHYTISM: TAXONOMIC PARTICIPATION AND ADAPTIVE DIVERSITY[1]

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ABSTRACT

Vascular epiphytes share few qualities beyond occurrence in tree crowns that identify them as a single ecological type, primarily because their phylogenetic origins and life styles in forest canopies are diverse. Mineral ion procurement by epiphytes is sometimes novel, often requiring trophic mutualism and unusual substrata. Patterns of moisture and nutrient use are, on the whole, not unlike those of terrestrials native to comparably arid or infertile sites. Moisture supply, more than any other feature, determines where a particular type of epiphyte will survive. Epiphytes constitute about 10% of all vascular species; the group is dominated by higher ferns and relatively few angiosperm taxa. Factors that probably predisposed ancestors of such modern clades as ferns, bromeliads, and orchids for epiphytism are identified. Reasons for the disproportional representation of certain dicot families in tree crowns are less clear, but some possibilities are offered. Constraints centered on water relations and, indirectly, mineral nutrition may explain why epiphytism has rarely, if ever, preceded branch parasitism.

EPIPHYTISM: DEFINITION AND BREADTH

Epiphytes are plants that spend much or all of their lives attached to other plants. Qualifying forms range from microbes to angiosperms; both aquatic and terrestrial vegetation provide mechanical support. Interaction with phorophytes can range from incidental to physiologically intimate; primarily rain-fed "atmospheric" bromeliads and orchids (Figs. 3, 4) are anchored by a few roots (sometimes only one), whereas contact is almost complete for the largely endophytic dwarf mistletoes. (The designation "epiphyte" is here reserved for free-living vascular species; it does not include hemiparasites.) This report has two purposes: to describe taxonomic participation in epiphytism and to explore the extraordinary proliferation in arboreal habitats by some families and higher taxa. First, epiphytes are examined in terms of basic characteristics and important biological distinctions.

Plants considered to represent a specific ecological category usually share key qualities that

set them apart from other vegetation. Occurrence on the same general type of substratum and, more importantly, utilization of comparable resource bases by similar mechanisms require considerable, often conspicuous, convergence. All botanical carnivores possess traps designed to attract and process fauna for food; all lianas feature slender habit and novel vascular anatomy; all vernal ephemerals from temperate deciduous forests generate simplified shoots bearing heliophilic, short-lived foliage. In contrast, anchorage in tree crowns—sometimes even inability to survive terrestrially—exhibited by so many of the approximately 25,000 epiphytic species appears to have little unifying basis. No growth form, seed type, identity of pollen vector, water/carbon balance regimen, source of nutrient ions, nor resource procurement mode is shared by all mechanically-dependent species. Moreover, characteristics of epiphytic and soil-based flora overlap broadly, as do important aspects of their habitats.

Growing conditions for epiphytes, as indicated by rooting media, microclimate, and stability and dispersion of substrata, are diverse and similar to those for much terrestrial vegetation. Like soils, which range from equable to dry and infertile, canopies of everwet to microphyllous to cactus forests impose mild to severe stress on resident flora. Problems of anchorage and dispersal in tree crowns are probably similar to those experienced by cliff dwellers and plants native to other precipitous sites. A naked bark surface must complicate water and mineral balance just as do thin soils and rock faces. At the other extreme, however, the everwet forest's rotting trunks or branches (Fig. 2), debris-filled knotholes, and ant nests (Fig. 7) probably offer to certain humiphilous epiphytes resources equal to those available at humid, fertile, terrestrial sites. In effect, heterogeneity and similarity to other habitats complicate definition of the epiphytic biotope and thwart attempts to understand why tree crowns offer the only recourse to such a variety of vascular plants. From another vantage point, canopy-dependent species seem to be no more versatile than soil-rooted plants; most will survive only under narrowly proscribed circumstances (e.g., rigid confinement to twigs rather than larger axes, humus as opposed to "unconditioned" bark, dark instead of better-illuminated sites).

Many taxonomies have been formulated to classify mechanical dependence. Criteria most often used are extent of arboreal presence (facultative vs. obligate forms), nature of dependency on supporting vegetation (mistletoes vs. epiphytes), exposure requirement (heliophiles vs. sciophytes), habit (e.g., tank forms, myrmecophytes), and type of substratum (e.g., humiphobes, ant-nest forms). A further criterion recognizes two types in a special group that normally taps soil part of the time—the hemiepiphytes. Primary hemiepiphytes, a group which includes stranglers, begin life on bark and later produce soil roots; secondary hemiepiphytes (Fig. 11) germinate on the ground and then become canopy-dependent as older roots and basal stems of vining shoots decay. Features more directly reflecting peculiarities of vegetative function associated with epiphytic life (e.g., presence of absorptive trichomes, carbon fixation pathway) have not generally been employed to distinguish epiphytic vegetation despite their utility for explaining type of microsite and how existence in that kind of space is sustained.

One criterion above all others may prove meaningful to those concerned with the mechanics of epiphytism: temporal access to moisture. While adequate mineral nutrition and exposure are no less critical than are suitable water relations to long-term survival of an epiphyte, avoiding drought injury is the more immediate challenge. Constant adjustment to rapidly changing moisture supply must be accomplished via appropriate stomatal and photosynthetic responses. There are just two types in this new taxonomy: continuously-supplied (CS) and pulse-supplied (PS) forms. Moisture supplies are steady for CS species tapping deep, absorbent media (Figs. 2, 5) or catchments created by the plant itself (Figs. 8, 9). The most self-contained members of the canopy-dependent flora (PS epiphytes) draw water from relatively nonabsorbent substrata or other sources subject to quick drying (Figs. 3, 4).

Epiphyte life history has been influenced by many selective forces, including substratum distribution and stability. Patchiness in the epiphytic biotope ranges from gross patterns due to hyperdispersion of tropical-forest trees to finer-grained discontinuity in the scattered arrays of suitable bark within individual hosting crowns. Mortality continues to be high during and following seedling establishment. Disturbance is lethal when supporting bark fragments exfoliate, inhabited twigs fall, infested trees collapse, and (less common but broader in extent) natural dis-

FIGURES 1–4.—1. Partially dissected shoot of the bromeliad *Brocchinia tatei* on Cerro Neblina, Venezuela, exposing rhizomes bearing traps of *Utricularia humboldtii*, a tank bromeliad endemic.—2. Young specimen of *Catasetum* sp. rooting in a rotting branch in Amazonas, Venezuela.—3. Scanning electron micrograph of the indumentum of *Tillandsia tectorum*, an atmospheric bromeliad. Inset illustrates habit.—4. Fruiting specimen of *Campylocentrum pachyrrhizum* and two small bromeliads growing on a small branch in south Florida.

asters ravage whole communities. Effective patch life (patch duration relative to the interval needed for a resident plant to reproduce) must be especially short for a multitude of epiphytes whose fecundity is limited by drought and poor nutrient sources. It is this group that possesses an unusual combination of stress and r-selected characters (Benzing, 1978). In contrast, CS species, with their relatively regular resource supplies, should exhibit less emphasis on shortening the life cycle and channeling scarce commodities into reproductive rather than vegetative tissue.

Adaptive Variety in Canopy Dependents

Some adjustments to conditions in tree crowns are predictable and obvious—viz. capacities for aerial dispersal and holdfast—but others are more cryptic and varied. Depending on taxon and habitat, epiphytes exhibit various mechanisms for carbon fixation and procurement of moisture and nutrients. Essential elements are drawn from remarkably diverse sources, including several not normally available to plants. A survey in some Indian forests (Sengupta et al., 1981) revealed greater nitrogenase activity in the phyllosphere of epiphytes than of terrestrials, including hosting trees. Impoundments built of roots or shoots provide access to nutrients via intercepted canopy fluids and litter (Figs. 8, 9) and the necessary detritivores and saprophytes these catchments attract (Benzing, 1986a). Carnivory is rare in the epiphyte synusia (Fig. 1), while trophic myrmecophily (Fig. 12) is common and may, in fact, be entirely restricted to canopy habitats (Thompson, 1981; Givnish et al., 1984). Where substrata are deeply penetrable and moist, absorptive organs and nutrient supplies are more conventional. It is not known whether epiphytes possess special permeabilities to match the character of the media (organic and acidic) they so often exploit.

Water/carbon balance is also assured by considerable mechanistic variety. At one extreme, some canopy-dependent pteridophytes alternate between wet-active and dry-inactive states as microclimate dictates. Quite the opposite, impoundments provide continuous drought relief for hundreds of species of bromeliads (Fig. 8), fewer orchids, some other monocots (Fig. 9), and ferns. Turnover of the entire leaf surface cued by impending seasonal drought is exemplified by members of several orchid genera (Fig. 2). Crassulacean acid metabolism (CAM) may be better represented in the forest canopy than in any other habitat type; stable carbon and hydrogen isotope data as well as more direct measurements of fixation pathway indicate that every known variation on this mechanism exists in epiphyte flora. Occasional subjects—the shootless orchids, for instance—exhibit novel machinery for gas exchange (Cockburn et al., 1985). Unusual osmotic qualities and related stomatal sensitivities appear to rank among the most unique of the functional peculiarities of epiphytism (Benzing, 1986a). Survival is often predicated on extensive storage capacity, economical water use, and ability to rebound rapidly from drought-imposed stress. Water balance is aided by special absorptive tissues that prolong contact with transitory fluids via mini-impoundment (e.g., the velamen of orchid roots; Fig. 10; Benzing & Pridgeon, 1983). Like other stress-tolerant plants, PS epiphytes grow slowly, a characteristic which moderates resource requirements but heightens vulnerability to habitat patchiness, disturbance, and other phenomena that oblige heightened fecundity.

Habits of epiphytes are often specialized in ways other than those associated with impoundment and myrmecophily. Abbreviation and merger of functions is common in the especially xerophytic forms, particularly the PS epiphytes; the most spectacular reductions occur in Bromeliaceae and Orchidaceae (Benzing & Ott, 1981). Within Tillandsia/Vriesea, root development has been almost completely suppressed and paralleled by complementary shoot modification. Just about every intermediate condition between profuse and very sparse rooting exists throughout the complex of more than 500 species. Corresponding shoot changes center on a progressively diminished impoundment capacity and an indumentum elaborated to the point where, among atmospheric forms, absorbent trichomes densely cover all foliar and most stem surfaces (Fig. 3). At this stage of specialization, no other organs are needed for uptake function. Orchidaceae (subtribe Sarcanthinae) exhibit a comparable progression except that here a telescoped, leafless shoot now supports production of green roots and the periodic axillary scape (Fig. 4).

The loss of axial differentiation seen exclusively in PS epiphytes may not be coincidental. Species that grow attached to impenetrable media or hang free in the atmosphere occupy habitats as uniform as those colonized by prevas-

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Figures 5–8.—5. A mixed colony of angiospermous epiphytes rooted in deep humus on a palm on Cerro Neblina, Venezuela.—6. A dense growth of bryophytes supporting shade-tolerant hymenophyllaceous ferns at the base of a tree in undisturbed lowland rain forest in Amazonas, Venezuela.—7. Seedlings of epiphytes rooted in ant-nest carton in lowland Venezuelan rain forest.—8. Tillandsia utriculata, a tank bromeliad, in south Florida.

VELAMEN

EKODERMIS

CORTEX

STELE
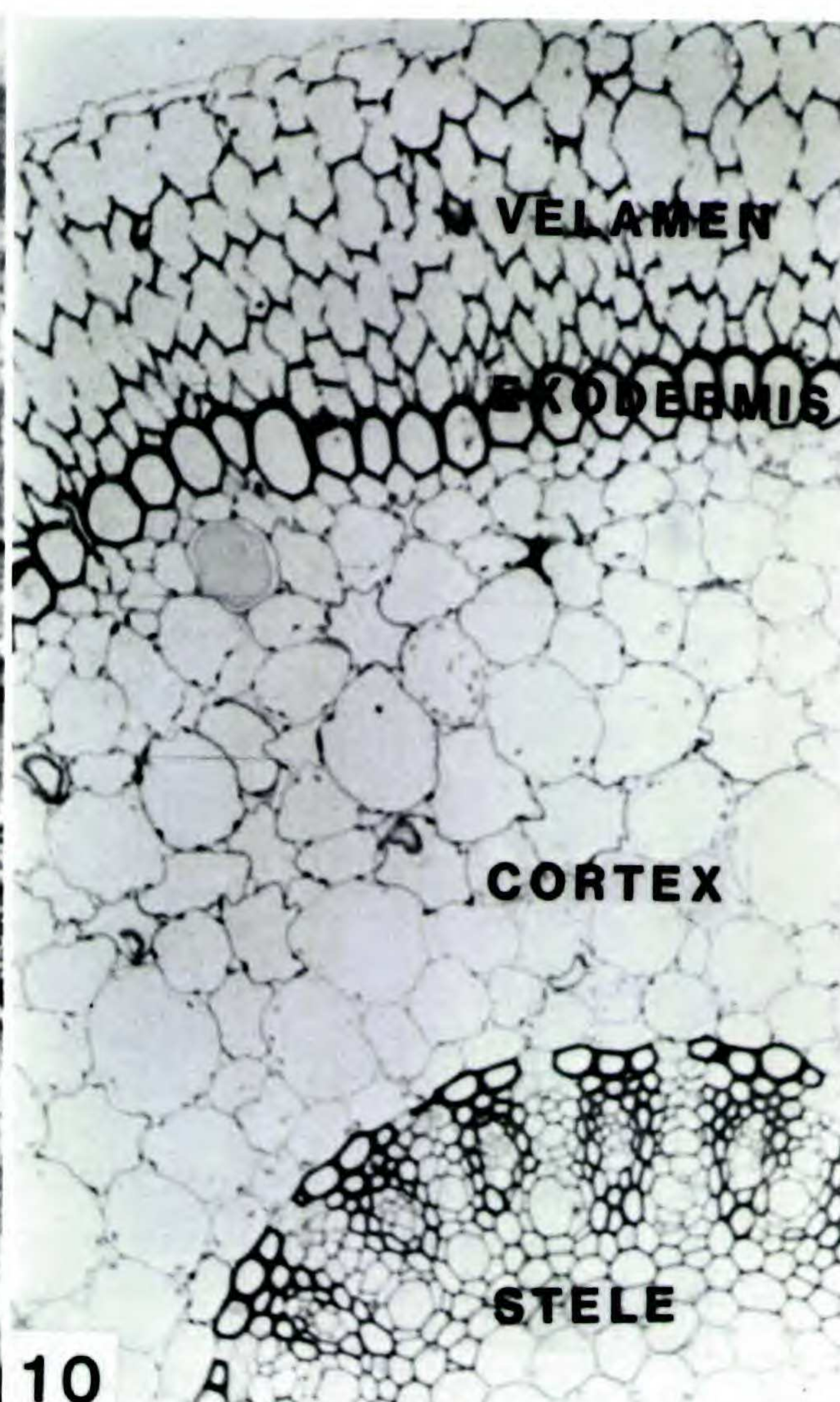
cular plants or modern aquatics. In such an environment, PS epiphytes need not maintain the division of labor between shoot and root that would be required for life on soil and, in fact, may sacrifice fitness by retaining a body plan inherited from terrestrial ancestors. Material and energy economy accompanying amalgamation of vegetative function in a single organ system while other parts are lost may promote fitness where stress and high mortality place a premium on fecundity. Complex functional tradeoffs obliged by extreme habit reduction in Bromeliaceae and Orchidaceae have been described elsewhere (Benzing & Ott, 1981; Benzing et al., 1983). Somewhat less spectacular abbreviations leading to single-leaf ramets parallel increased exposure and stress tolerance in additional, predominantly epiphytic, orchid lines (e.g., *Dendrobium, Epidendrum*).

Although extensive studies have been made of orchid pollination, seed germination, and seedling nutrition, and some work has been done on mistletoes (e.g., Bernhardt, 1983), bromeliads (Smith & Downs, 1974), and a few other epiphytes, life history characteristics of canopy-dependent vegetation as a whole remain obscure. What data are available indicate that nonuniformity is the rule once again. An exception is the usual pattern of extended iteroparity; only a few *Tillandsia* and *Vriesea* species flower just once. Pollinators include all the common vectors except wind. Because air turbulence is adequate to disperse most epiphyte seeds despite their greater mass compared with pollen, absence of wind pollination must relate to other factors, most likely to the expense of required reproductive material or hyperdispersion of populations. Syndromes featuring specialized animals or unusual foraging activities are more common here than in other tropical synusiae. Breeding systems vary from those obliging strict outcrossing via trapliners to autogamy. Some minor patterns may be emerging, however. Orchids seem to be predominantly allogamous, while many ant-nest inhabitants and Marcgraviaceae are selfers (Gentry & Dodson, 1987). The widely-held view that, on average, epiphyte populations are more frag-

mented than those of terrestrials and hence subject to special genetic structuring and propensity for cladogenesis needs to be verified. If they are not, neither a uniform nor unique reproductive pattern should be expected.

Seed is dispersed by various agencies. Among families, the vectors are most often animals (via fleshy fruits), but when species are counted, anemochory ranks first owing to the immensity of the Orchidaceae. Among wind-borne species (more than 80% of the total), seeds bearing elaborate appendages are uncommon. Attempts to relate seed form and mass to mobility in aerial habitats can be complicated because disparate agents sometimes provide service for the same species. *Dischidia* seeds bear a plumose coma but also an oily eliasome to attract ants (short-range vectors; Docters van Leeuwen, 1954). Nest-inhabiting *Codonanthe* has a fleshy berry containing myrmecochorous seeds. Other subtleties of epiphytic reproduction are just as easily overlooked—one flat side on otherwise fusiform *Hydnophytum* seeds reduces vulnerability to dislodgement by stemflow (pers. obs.). Seed size differential between terrestrial and epiphytic relatives is not consistent. Madison (1977) reported more massive seeds in soil-based compared with canopy-based Araceae and Cactaceae, but epiphytic gesneriads definitely do not produce lighter seeds than do numerous terrestrial relatives (H. Wiehler, pers. comm.). Surprisingly, microsperms of terrestrial orchids are more buoyant than those of test epiphytes (Stoutamire, 1974). Rockwood's survey (1985) of 365 species in eight families from diverse communities in Costa Rica, Panama, and Peru yielded additional, unexpected results. Average seed mass of 59 epiphytes (orchids excluded) was lighter than that of tree seeds but heavier than that of terrestrial herbs and shrubs.

Table 1 tabulates angiosperm families containing more than 50 epiphytic species and lists characteristics that contribute to their success in tree crowns. Figure 13 summarizes adaptive diversity within free-living, canopy-dependent, vascular flora relative to local moisture supply. Species with character states assigned to the far

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FIGURES 9–12.—9. A "trash basket" *Anthurium* in lowland rain forest in Amazonas, Venezuela.—10. Cross section through the root of *Epidendrum radicans* illustrating the major tissues, ×250.—11. Hemiepiphytic aroid in rain forest at Río Palenque, Ecuador.—12. *Hydnophytum formicarium* illustrating ant-accommodating cavities within the swollen hypocotyl.

FIGURE 13. Occurrence of character states of vascular epiphytes according to moisture availability in microhabitats. See text for details.

right of the grid (indicated by lines) are usually PS types. Those on the extreme left experience continuous supply punctuated only by the uncommon, normally brief, drought. Epiphytes bearing character states assigned predominantly to the left or right of Figure 13 can occur together. Pulse-supplied and CS forms inhabit humid sites, although only PS epiphytes occupy tree crowns in drier locations. Twig and free-hanging "mist" types in rain forests, for instance, receive moisture and nutrients exclusively via periodic flow, so their supply is intermittent. A nearby tank or humus epiphyte experiences considerably less discontinuity between rain events. Species situated on highly exposed sites in humid forests or on most anchorages in arid woodlands exhibit slow growth, long-lived photosynthetic organs, and foliar or root surfaces modified to prolong contact with passing fluids (i.e., thick velamina or absorbing trichomes). Vegetative bodies are often much abbreviated, another means of improving economy. Woodiness seems to be sustainable only where moisture is abundant.

Features associated with regular resource supply are diverse. Hemiepiphytes are continuously supplied, at least while rooted in soil; habits may be woody or herbaceous. Nutrient ions are drawn from various types of humus by roots and absorptive leaves of various CS forms. Carnivory is possible for the tank former. Ant-nest gardens are scarcer in the drier forests, but trophic myrmecophily is widely available. Too little is known about mycorrhizae and nitrogen nutrition in the mechanically-dependent synusia to posit their incidence in Figure 13, although humidity promotes microbial activity elsewhere. The C_3 photosynthetic pathway, first supplemented with CAM-cycling and then ever greater reliance on nocturnal fixation, seems to play a diminishing role from left to right. Precise ordering of CAM variations in Figure 13 and the proposed significance of CAM-cycling as a mechanism that "poises" the plant for drought (Ting, 1985) should be considered provisional at this time. Poikilohydry is feasible only on relatively humid sites for reasons described below. Deciduousness (e.g., *Catasetum*; Fig. 2) occupies an intermediate position, occurring where drought is predictable (seasonal) and not too severe. High solute potential has been documented among CS and PS epiphytes (Harris, 1918; Spanner, 1939; Sinclair, 1983) although its effect on stomatal sensitivity has not been examined extensively. Vegetative features seem to have no bearing on type of pollinator used. Dispersal syndromes correlate only weakly with habitat humidity or resource procurement mechanisms. Anemochory is found everywhere, but a pulse-supplied nature increases the probability that an angiosperm will be wind-dispersed. Propagules that pass safely through a bird's gut are generally larger (more expensive) than the smaller anemochores, a relationship that may help explain why wind-dispersed *Tillandsia* and Orchidaceae dominate the most stressful epiphytic habitats. Without small seeds, low productivity would probably result in low generative capacity for the PS epiphyte. The few monocarpic bromeliads are relatively well-provisioned impounders rather than stress-tolerant atmospherics; the latter's resource procurement capability is probably inadequate to support semelparity (Benzing & Davidson, 1979).

In summary, epiphytes engage in a broadly similar rather than a narrowly proscribed way of life. Many other ecological groups are better defined because members subjected to less varied environmental constraints conform to more coherent adaptive syndromes. Inconsistency in the epiphyte synusia is a function of habitat breadth (numerous possibilities for adaptive specialization) and the multiple phylogenetic origins of tree crown occupants. More than one character combination can be associated with specific types of rooting media and climates, and no single key feature or suite of features is evident. Vegetative phenomena that seem to be proportionately better represented in canopy- than in soil-dependent floras include various types of nutritional symbioses, creation of soil substitutes, slow growth, evergreenness, CAM, special absorptive tissues, and abbreviated habits. Most specialized of the epiphytes are the PS species because they are most vulnerable to drought and substratum patchiness and disturbance. Modes of pollen and seed conveyance are also various among epiphytic plants, with few, if any, characters unique to these taxa. Indeed, most features of canopy-dependent plants occur among terrestrial flora as well, although not necessarily in the same combinations.

SYSTEMATIC OCCURRENCE AND THE MULTIPLE ORIGINS OF EPIPHYTISM

Approximately 10% of all vascular plant species are at least occasionally epiphytic, but distribution among higher taxa is uneven (Gentry & Dodson, 1987). Broad involvement is particu-

TABLE 1. Preliminary tabulation of predominantly vegetative features underlying the epiphytic habit in angiospermous families containing more than 50 canopy-dependent species. Common and less frequent strategies for canopy life are also included.

Group or Family	Habitat Humidity	Most Pervasive Adaptive Features	Less Pervasive Adaptive Features	Common Ecological Types	Minority Ecological Types
Ferns	Wet to moderately dry	Dust-size propagules; poikilohydrous tendency; shade tolerance; diverse habits	Macroimpoundment: brood chambers for ants; CAM; pronounced resurrection capacity; absorbing foliar trichomes	General humus-rooted, sciophytic epiphytes	Trophic myrmecophytes: resurrection forms; drought-enduring, CAM forms, trash-basket epiphytes
Araceae	Wet	Vining habit; macroimpoundment; microimpoundment (velamen); plastic foliar form	Deciduousness	Secondary hemiepiphytes; trash-basket and general humus-rooted epiphytes	Nest-garden epiphytes
Bromeliaceae	Wet to dry	Macroimpoundment; microimpoundment (foliar trichomes); CAM; vegetative reduction; xeromorphy	Carnivory; brood chambers for ants; deciduousness	Tank epiphytes; PS epiphytes (atmospherics)	Nest-garden and general humus-rooted epiphytes; trophic myrmecophytes; drought avoiders
Orchidaceae	Wet to dry	Microimpoundment (velamen); CAM; vegetative reduction; microsperms; xeromorphy; fungus-assisted juvenile nutrition; mycorrhizae (?); diverse habits	Macroimpoundment; brood chambers for ants; deciduousness	General humus-rooted epiphytes; PS epiphytes (drought-enduring CAM forms)	Trophic myrmecophytes; nest-garden epiphytes; drought avoiders
Araliaceae	Wet	Versatile root growth and function		Woody hemiepiphytes	General humus-rooted, shrubby epiphytes
Asclepiadaceae	Wet	Vining habit; CAM; xeromorphy; various ant associations		Vining, often humus-rooted epiphytes	Trophic myrmecophytes
Cactaceae	Wet to dry	CAM; xeromorphy		Secondary hemiepiphytes; general humus-rooted epiphytes	
Clusiaceae	Wet	Versatile root growth and function	CAM; xeromorphy	Woody, primary hemiepiphytism, occasionally stranglers	General humus-rooted, shrubby epiphytes

TABLE 1. Continued.

Group or Family	Habitat Humidity	Most Pervasive Adaptive Features	Less Pervasive Adaptive Features	Common Ecological Types	Minority Ecological Types
Ericaceae	Wet	Mycorrhizae (?); preference for acid, organic, oligotrophic substrata (?)		General humus-rooted, shrubby epiphytes	
Gesneriaceae	Wet to moderately dry	CAM; xeromorphy; various ant associations; diverse habits		General humus-rooted epiphytes	Ant-nest epiphytes
Marcgraviaceae	Wet	Vining habit; plastic foliar form		Secondary hemiepiphytism	
Melastomataceae	Wet	Preference for acid, organic, oligotrophic substrata (?)		General humus-rooted, shrubby epiphytes	Hemiepiphytes
Moraceae	Wet to moderately dry	Versatile root growth and function; strangling habit		Stranglers	
Piperaceae	Wet	CAM; xeromorphy; small size		General humus-rooted epiphytes	
Rubiaceae	Wet	CAM; xeromorphy; brood chambers for ants		Myrmecophytes; humus-rooted epiphytes	

larly apparent at the higher taxonomic levels. Fully 44% of all vascular plant orders and 16% of families (sensu Cronquist, 1968) contain one or more tree-crown populations. Arboreal monocots far outnumber dicots, even exceeding Filiopsida (44 vs. 27%) for proportional occurrence in forest canopies. Of the two large lycopod genera, *Lycopodium* is about one-third epiphytic (143 spp.) while *Selaginella*—a considerably larger, heterosporous group—contains only five such species (Beitel, 1979). A majority of Psilotophyta regularly inhabit tree crowns. Gymnosperms, on the other hand, are largely confined to soil, in part no doubt because of their heavy seeds and costly wind pollination. Orchidaceae have been more successful than any other lineage in canopy habitats. Two out of three epiphyte species are orchids; about 70% of the family is canopy-dependent. Two other large monocot groups with a pronounced epiphytic bias are Araceae, especially *Anthurium, Philodendron,* and *Rhaphidophora,* and Bromeliaceae, more than half of which anchor on bark. Canopy-dwelling dicots are disproportionally represented by Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae, Moraceae, Piperaceae (specifically *Peperomia*), and Rubiaceae. Versatility within participating clades is not consistent. Component taxa may be diverse or uniform in the mechanisms that foster habitation in tree crowns (Table 1).

In all, about 80 vascular families contain at least one canopy-dependent member, but there are conspicuous, occasionally puzzling, omissions. Some very large, ecologically diverse groups with numerous tropical members are little represented in, or even absent from, canopy floras. Leguminosae may be constrained by fruit and seed types that offer little potential for aerial dispersal. Poaceae (and all Cyperales) may be almost entirely terrestrial owing to consistent wind pollination and the graminoid habit, which does not lend itself to evergreen drought endurance. Plausible reasons for the paucity of epiphytes within the immense Asteraceae are not so obvious; both CAM-assisted xerophytism and wind-dispersed seeds are well developed in parts of this family. These exceptions notwithstanding, angiospermous epiphytes are concentrated in the more advanced taxa. The same is true of ferns, but again, there are exceptions. Two members of the primitive order Ophioglossales root in humus impounded by persistent palm leaf bases

and *Platycerium* fronds. If *Psilotum* and *Tmesipteris* of the bigeneric Psilotophyta are indeed sole remnants of the Silurian/Devonian psilophyte complex, epiphytism is possible for the most primitive vascular relics.

Epiphytism has probably evolved independently from terrestrial stock in every participating family of seed plants and most families of ferns. It has arisen more than once in most of those spermatophyte taxa containing canopy-dependent species on different continents (Gentry & Dodson, 1987), indicating that propensity for arboreal life is rather fundamental in some major clades. Most diverse of the epiphyte types, phylogenetically speaking, are the humiphiles whose drought liability obliges access to moist organic debris such as that covering older bark exposures in everwet forests. Virtually every family containing epiphytes includes at least one such species; most contain no other type. Where more exacting conditions (e.g., exposed bark and twig surfaces) prevail, few families are represented, although these are sometimes speciose (Benzing, 1978). Neotropical ant nests provide specialized substrata for a small myrmecochorous flora which often offers extrafloral nectar. Perhaps additional traits as yet unrecognized that might affect capacity to root in cartons are mostly limited to Araceae, Bromeliaceae (specifically subfamily Bromelioideae), Cactaceae, Gesneriaceae, Marcgraviaceae, Orchidaceae, and Piperaceae. Some Asclepiadaceae, Melastomataceae, and Rubiaceae are part of similar but less well-defined symbioses in Australasia (Janzen, 1974). Those trophic myrmecophytes that exhibit unequivocal modifications for ant occupancy all belong to Asclepiadaceae, Bromeliaceae, Melastomataceae, Orchidaceae, Polypodiaceae, and Rubiaceae (Huxley, 1980). Rubiaceae seem to be most specialized for the relationship (Fig. 12). Stranglers—about 300 in all—come from just eleven families of dicots, most notably Moraceae (*Ficus*). Secondary hemiepiphytes have vining habits, and indeed the majority belong to groups with a scandent tendency (e.g., Araceae, Cyclanthaceae, Marcgraviaceae). Bromeliaceae largely account for the tank formers (Fig. 8). Trash-basket habits (Fig. 9) are present in a modest number of families; the numerous PS epiphytes are almost exclusive to Bromeliaceae (mostly *Tillandsia*) and Orchidaceae (many subtribes).

Both parallelism and convergence have fostered much redundancy in the rise of epiphytism. Par-

allelism is illustrated by CAM, which features a key mechanism (incorporation of CO_2 via β-carboxylation) fundamental to regulation of ionic and osmotic balance through metabolism of malate and perhaps other organic ions (via a biochemical pH-stat). Heightened enzyme activity, appropriate malic acid mobility and storage capacity, phase-shifted stomatal behavior, and other associated characters enabling high water use efficiency have emerged in close to 30 families and more than once among some of those containing epiphytes—Bromeliaceae and Orchidaceae, for instance. Inherently slow relative growth rates, great longevity of whole plants and their individual parts, along with underlying oligotrophic physiology in canopy- and soil-based vegetation alike, probably also reflect common potential realized under similar selective impetus. Somewhat more unique features based less on homology than on novel design opportunity are, among others, devices to effect impoundment and/or accommodate ant occupancy. On balance, mechanisms governing resource use appear to be based on relatively few, widely available, genetic foundations, while functions and structures effecting resource procurement have more numerous and varied origins, likely based on convergence.

PREDISPOSITION AND ADAPTIVE CANALIZATION

Compared with vertebrates, vascular plants exhibit great adaptive fluidity. While mammalian radiation has conformed to body plans and dietary patterns established early in the group's history, botanical taxa of comparable rank exhibit varied habits, tolerances, and life histories. Quite commonly, natives of disparate habitats even belong to the same genus. Difference in evolutionary pattern partly reflects the higher plant's greater physiological plasticity aided by continuous turnover of both vegetative and reproductive organs. Selection may occur among ramets—perhaps even tissues within individual organs—during the life of a single clone (Walbot & Cullis, 1985). Evolutionary tempo is rapid enough to effect speciation in as little as 10^4–10^5 years—or perhaps a few decades!—in Orchidaceae (Gentry & Dodson, 1987). Reputedly, only a small number of genes need to be involved to alter structure, function, and ecological tolerance (Gottlieb, 1984; but see Coyne & Lande, 1985).

Some angiosperm lineages are quite conservative, however, as if for them, too, entry into certain adaptive zones restricts access to others.

Cases of evolutionary canalization abound in Magnoliophyta. Somatic conservatism is frequent within genera and an invariant adaptive mode can typify entire, albeit small, specialized families (e.g., Sarraceniaceae, Lemnaceae). More impressive evidence for constraints on direction but not speciation in plant evolution is provided by greater redundancy in other families. Examples include halophytism in Chenopodiaceae, ruderalism in Brassicaceae, drought-enduring xerophytism in Cactaceae and, of course, epiphytism in Orchidaceae. No single life style characterizes the entire clade in any of these examples, but particular themes turn up too often to deny underlying family-wide dispositions. Success in a particular environment is predicated on a novel set of features that imparts ability to counter major external constraints. Once the essential components were perfected and integrated, whether by serendipity or some optimizing mechanism, each ancestral stock became better equipped to enter one, and less so another, adaptive zone. Since accessible space was widely available in each case, considerable cladogenesis followed, sometimes through agencies unrelated to vegetative performance, hence native substratum. Orchidaceae achieved unequalled speciation in humid, neotropical forest canopies because of behavior peculiar to male euglossine bees.

Adaptive syndromes are comprised of structural, functional, and phenological components which can be identified through consistent occurrence in participating species. Ruderals succeed through their capacity to create seed mass rapidly, because time is the major constraint affecting success in resource-rich, disturbed habitats. Components of this well-defined syndrome are: habits incorporating minimal mechanical and root tissue; vigorous photosynthetic machinery; small, long-lived, often light-sensitive, propagules; and self-compatibility. Here, such traits as low shoot/root ratios, woodiness, and extensive succulence are never found because they are inconsistent with ephemeral life histories. Although the habits of vascular halophytes range from large trees (mangroves) to succulent terrestrial and submerged herbs, certain physiological phenomena are common to all because potential for desiccation is always one of the predominant

problems in saline media. Osmotic compensation and compartmentation of specific solutes provide the only means for maintaining water relations in hyperionic habitats. In every case, potentially toxic ions, taken in from the environment to lower tissue water potential, must be sequestered in vacuoles at concentrations above those encountered in glycophytes, and they must be balanced across the tonoplast by osmotica of plant origin. Salt balance can be fine-tuned further by taxon-specific features. Chenopod halophytism is aided in salty surroundings by multicelled vesicular hairs which excrete excess Na^+ and Cl^-; succulence provides for ion dilution. The presence of organic solutes, including proline, in other salt-tolerant taxa instead of the betaines found in Chenopodiaceae reveals that physiological convergence among natives of saline environments is not complete. Likewise, the abundant malic acid synthesized by all CAM plants at night for subsequent daytime generation of an internal CO_2 supply is usually decarboxylated through only one of the three existing reactions: mediation by NAD- or NADP-dependent malic enzyme or PEP carboxykinase.

On balance, floristic variety generally reflects the equability and heterogeneity of a particular adaptive zone, all other variables being equal. Fertile, moist soils and abundant light have fostered wide convergence—ruderals are a good example. Weeds in crop fields belong to many families, reflecting easy access to a collection of required character states. Tropical forest canopies have been similarly colonized but only to a certain degree. Whereas many lineages have evolved traits that allow growth on the organic arboreal "soils" of everwet forests, few have invaded more demanding zones, as demonstrated by narrower taxonomic participation in PS epiphytism (Benzing, 1978).

Inherited—in effect, phyletic—constraints determined which ancestors of modern families could generate epiphytic derivatives. Inherent barriers are complex and little understood, but their existence in plants is becoming recognizable (e.g., Kochmer & Handel, 1986; Hodgson & MacKey, 1986). Potential to express key components of an adaptive syndrome was not sufficient to assure its establishment. Universal occurrence of CAM-like function, for instance, did not guarantee adoption of CAM by all xerophytes nor by all aquatic macrophytes in the softwater lakes where nocturnal fixation is favored by limited carbon supply (Keeley, 1981; Richardson et al., 1984). Moreover, each character of a syndrome must be free of pleiotropic and linkage relationships with maladaptive or internally incompatible traits. Biomechanical compatibility is essential; for instance, plants with vigorous cambia may rarely employ CAM, probably because costly woodiness is not sustainable without greater capacity for carbon gain.

Little is known at this point about inertia in the genetic, epigenetic, and biomechanical interplay among phenomena responsible for salt balance in halophytes, resource uptake and processing in short-lived eutrophs, or water economy in CAM plants. But occurrence among related genomes does demonstrate that some characters affecting vegetative performance and thereby suitability in particular habitats—e.g., sites of nitrate reduction (shoot as opposed to root), ability to adjust osmotically under various degrees of stress, and presence of particular ion pumps and channels—can be more or less readily gained, modified, or lost. More narrowly restricted throughout Magnoliophyta, often to a single family or order, are features such as capacity to form a particular type of mycorrhiza, nodulate with *Rhizobium*, synthesize cardiac glycosides or betaines rather than anthocyanin pigments, and utilize sorbitol rather than sucrose for phloem transport.

Access to vital characters during plant evolution has been affected by related impacts on photon, water, and nitrogen use efficiency (Raven, 1985a). Constraints on evolutionary opportunity have been strongest where drought, shade, or infertile substrata accentuate premiums on water, energy, and nutrient economy respectively. Type of nitrogen source, for instance, imposes different demands, depending on where (in which organ) processing takes place, how much water and energy is needed per unit of product, and the environmental context (is light or moisture scarce or abundant?). Calculation of comparative costs must extend beyond inputs for chemical synthesis to include transport and pH regulation. Excess protons must be eliminated by users of NH_4^+ and N_2, while excess OH^- is consumed or excreted by NO_3^- assimilators. Although the ammonium-to-protein pathway is least expensive in terms of energy consumption, overriding factors may still dictate another choice even where NH_4^+ is in greatest environmental supply. Soil is the usual sink for H^+ generated by NH_4^+ use.

Indeed, owing to the immobility of protons in phloem, terrestrial plants process most of their acquired NH_4^+ in roots, a potential limitation with special relevance for epiphytism. If this is the universal rule, then what compensation, if any, accompanied root system reduction in advanced Bromeliaceae? Evidence indicates that NH_4^+ is the predominant form of nitrogen in at least some tropical-forest canopies (e.g., Curtis, 1946). Conceivably, the absence of similar morphological diminution in nonbromeliad lineages is in part related to their less flexible nitrogen metabolism, although the role bromeliad foliar trichomes have played in obviating absorption by roots cannot be ignored in such comparisons. Perhaps slow-growing plants like the atmospheric bromeliads metabolize N at such low rates that complications are avoided. Either the internal biochemical pH-stat is adequate for disposal or excess protons are dumped from trichomes when shoots are wetted.

Similarly, land plants have evolved several mechanisms to effect osmotic balance. Here, cost escalates with deployment of inorganic (e.g., Na^+, Cl^-), then organic nonnitrogenous, and finally nitrogenous solutes, especially on infertile media. Again, nitrogen is an important currency but perhaps no less so than the energy and water spent for its acquisition and processing. In a somewhat different vein, fungal biomass has to be supported by the mycorrhizal plant; but returns in phosphorus, and sometimes water and other nutritive ions, justify the investment in all but the most fertile habitats. Comprehensive cost accounting, through knowledge of functional incompatibilities and the hereditary and epigenetic phenomena controlling access to key traits, is necessary to interpret patterns of radiation. It is at these levels of plant performance that many of the tradeoffs, economies, and accommodations underlying the evolutionarily-stable strategy occur.

HISTORICAL BASIS FOR CANOPY DEPENDENCE

It is currently impossible to explain fully why one particular lineage developed canopy dependence while another did not. But partial answers are available in some cases; several of the more notable ones are discussed below. Four questions provide focus: Why are proportionally more ferns than seed plants epiphytic? Why do so many monocots, particularly orchids, dwell in canopies? Why have several families of dicots with no obvious advantage by basic habit or water balance profile succeeded so widely there? Finally, why is branch parasitism relatively uncommon?

Ferns. Homosporous pteridophytes are successful in tree crowns, where they usually occupy lower strata, because of small diaspores. A second, less obvious, factor is a capacity to tolerate substantial drying and deep shade. Poikilohydry is pronounced in exceptional taxa (*Polypodium polypodioides*), but many other filicaleans exhibit desiccation tolerance superior to that possessed by most seed plants. A fern's pattern of drought resistance, unlike that of most CAM plants, is particularly compatible with occurrence deep in the forest. For instance, ultrathin fronds of Hymenophyllaceae (Fig. 6) probably photosaturate at very low fractions of full insolation and they can survive considerable desiccation. Greater exposure might be tolerable, and upper as well as lower strata heavily colonized, but for the trade-off associated with poikilohydry. Resurrection is adequate for countering the occasional brief drought every humid forest experiences now and then, but frequent dehydration is another matter. A regulated water economy based on thick (expensive, opaque) epidermal barriers and greater diffusive control is critical on markedly arid sites because photosynthesis is more likely than is respiration to be curtailed by severe water deficits. Should moisture supply be too intermittent and poikilohydrous foliage dry too often, carbon balance tends to become negative (Benzing, 1986a). Raven (1985b) cited rates of physiological processes, including photosynthesis and transpiration at the low end of the ranges reported for tracheophytes, as a reason why ferns are so well equipped to inhabit shady, drought-prone locations.

Nevertheless, a modest invasion of drier locations has been possible for higher ferns. One enabling mechanism here is drought avoidance via seasonally deciduous foliage (e.g., *Phlebodium aureum*). Occurrence in some stressful Australasian sites is possible for evergreen *Pyrrosia* and its equally coriaceous relatives through an odd juxtaposition of structural and physiological characters. There are reports of CAM in *Drymoglossum piloselloides*, *Pyrrosia longifolia*, and *P. angustata* (Wong & Hew, 1976; Sinclair, 1983; Hew, 1984) along with drying character-

istics more reminiscent of a resurrection plant than a typical desiccation-resistant xerophyte. A thorough examination of ferns with regard to microclimates, substrata, and water and carbon relations in both gametophyte and sporophyte stages will be necessary to place discussion of the evolution of pteridophytic epiphytism on a firmer foundation.

Liliopsida as a whole. Orchids account in large measure for the immense numbers of epiphytic species, but monocots would be disproportionately common in tree crown habitats even without them. Bromeliaceae and Araceae rank second and third. The ratio of monocot to dicot species in tree crowns is 5 : 1, but it is 1 : 4 overall. Although Araceae, Bromeliaceae, and Orchidaceae are the most successful families in forest canopy habitats, there is no common adaptive theme. Two photosynthetic pathways in many variations, tank and trash-basket impoundments, myrmecophytism, foliar trichomes, velamentous roots, and virtually all the dispersal modes enabling arboreal existence occur in epiphytic monocots. A peculiar body plan, shared to some extent with the higher ferns but less so with dicots, may have offered special class-wide opportunity.

Monocots in particular, but dicots as well, are often sectorialized in the sense that individual shoots operate as collections of relatively independent, serially aligned, physiological units (IPUs; sensu Watson & Casper, 1984). Tracer studies have shown that meristems may receive fixed carbon mainly from nearby leaves, sometimes only those attached at the subtending nodes. Longitudinal segmentation seems to be more characteristic of dicots, and may also help explain why several different habits and associated ecological tendencies have been emphasized in one or the other of the two classes. Partitionment into vertical compartments is evidenced by movement of labeled photosynthate among leaves and associated buds along a single orthostichy. Xylem supply is similarly restricted. Secondary thickening may eventually obliterate conductive barriers to lateral flux imposed by the dicot primary body, particularly where eustelic stem vasculature is "open"—i.e., composed of discrete series of interconnected leaf traces (sympodia). But, as previously noted, woodiness imposes another set of limitations, especially in arid habitats. Monocots with their more reticulate "atactostele," best known today

in palms (a group portraying the "Raphis Principle"; Tomlinson, 1984), appear to possess unique capacity for functional integration on one hand and, on the other, habits that permit extensive vegetative renewal in mimimal space. Perhaps especially fortuitous is the unusual ability to coordinate remote sources and sinks, and a related capacity to localize effects of damage and maintain vascular supply to organs that a more rigid system might be forced to abandon or underutilize. This kind of flexibility was illustrated by some experiments with grasses when mature ramets, returned to sink status by shading or defoliation (e.g., Callaghan, 1984; Welker et al., 1985), remained alive rather than self-pruned, as commonly occurs in forest trees. Historically, integration of this sort may have fostered extraordinary architectural plasticity with special implications for novel evolution. Recall that several large epiphytic monocot lineages have undergone major vegetative reorganization unequaled in dicot counterparts.

The exceptionally well-developed horizontal segmentation just described was undoubtedly important in the evolution of stress-tolerant epiphytic monocots, perhaps ferns as well. The advantages of a rhizomatous sympodial habit and potential physiological autonomy of the single phyton (a morphological unit composed of a leaf and associated adventitious root(s), bud(s), and subtending stem segment) were most accentuated during orchid phylogeny. Sequential production of reduced shoots (in effect, shoots composed largely of single expanded phytons in extreme cases) is a recurrent theme in this family. Adult shoots of *Dendrobium ultissimum* consist of nothing more than strings of stubby, closely placed, leafless pseudobulbs. The broader suitability of architecture based on serial renewal via determinate shoots generated from closely-placed meristems is illustrated by occurrence beyond the monocots. Somewhat less condensed versions of the same general arrangement exist among mechanically-dependent dicots (e.g., some Gesneriaceae) and *Lycopodium*. Differentiation of roots into feeder and holdfast types (Fig. 9), a useful division of labor for the vine or epiphyte, seems to be more common in monocots than elsewhere.

Nonorchid monocots. Bromeliaceae, with far fewer species and almost exclusively neotropical distribution, nevertheless rival Orchidaceae for variety of epiphytic life styles. Tank habits have

evolved independently in two subfamilies, and in all three if *Brocchinia* is correctly assigned to Pitcairnioideae (Benzing et al., 1985). A rosulate shoot was required for each transference of absorptive role from root to shoot. Ancestry was apparently mesic in both Tillandsioideae and Pitcairnioideae; tank shoots are associated with C_3 photosynthesis in each subfamily. Bromelioideae, with about 500 species capable of creating soil substitutes in leaf bases, are fundamentally CAM plants. Specialization for PS epiphytism, in effect for greater stress tolerance, has proceeded farthest in Tillandsioideae by way of the derived atmospheric forms (Benzing et al., 1985). Here, absorbing trichomes (Fig. 3) are perfected to the highest degree whilst the vegetative apparatus is reduced to simplest form.

Epiphytic Bromeliaceae, more than most, were clearly adapted to endure rigorous conditions by the presence of a suitable epidermal appendage and habit in precursors. Here, epiphytism is based on a modified shoot (Fig. 8) with the foliar trichome as its keystone feature (Table 1). Absorptive function might be possible in glabrous leaf bases when long-term contact with moist, nutritive tank fluids is maintained, but the rapid uptake required to sustain a rootless, nonimpounding PS bromeliad would be impossible without an extraordinary foliar indumentum. Myrmecophytism, and perhaps a single case of carnivory (*Catopsis berteroniana*; Givnish et al., 1984), are also associated with specialized trichomes and inflated leaf bases (Benzing, 1970). Hypotheses concerning how the bromeliad foliar epidermis may have acquired its current function and importance are described elsewhere (Pittendrigh, 1948; Benzing et al., 1985). (Briefly: contrary to Pittendrigh's proposition that absorptive function would only emerge under drought selection, Benzing et al. posited a mesic, infertile, ancestral habitat where the foliar epidermis evolved primarily to promote acquisition of nutrient ions from impounded humus or perhaps animal prey.) Bromeliad seeds are disseminated by birds (Bromelioideae) or wind (Pitcairnioideae and Tillandsioideae). Pollination syndromes are diverse and apparently not associated with either tank or atmospheric habit.

Aroid, by comparison with bromelioid or orchidoid, epiphytism is neither as advanced nor as versatile. There are no reports of CAM here, and overlapping foliage that might mitigate drought lacks the water-tight quality possessed by inflated bromeliad leaf bases. Trash-basket catchments (Fig. 9) sometimes trap falling litter but little moisture. Roots fail to produce velamina as elaborate as those serving the most drought-tolerant Orchidaceae, nor is there any indication that these organs can match foliage in photosynthetic vigor. Seasonally deciduous leaves on green or tuberous stems occur in *Philodendron* and *Remusatia* respectively, but these are minor themes with few participating species. Arboreal existence in Araceae is based predominantly on two mechanisms, both humus-based: impoundment, seen in short-stemmed *Anthurium* and some *Philodendron* (Fig. 9); and secondary hemiepiphytism (Fig. 11), a more widespread phenomenon most often encountered in *Philodendron*. Velamentous roots, and rosulate and vining habits incorporating progressive dieoff of proximal stem regions, appear to be the central vegetative features responsible for aroid expansion in canopy habitats (Table 1). Both sympodial (e.g., *Philodendron*) and monopodial (*Pothos*) habits are found in the hemiepiphytes. Ant nests are utilized by some *Anthurium* and *Philodendron*. Water and nutritional relations exhibit no obvious unusual modifications for arboreal life, but neither have been examined closely. Baccate fruits are an integral part of the syndrome, but they occur throughout the family without habitat restriction. Pollinators range from beetles to euglossines. Specialized pollen vectors may have encouraged enlargement of *Anthurium* and possibly other genera. Cyclanthaceae, the only other nonorchid monocot family with a sizable epiphyte contingent (about 66% of *Asplundia*), mostly penetrate the forest canopy as rooted climbers and secondary hemiepiphytes. True epiphytism occurs in *Sphaeradenia* and *Stelestylis* (G. Wilder, pers. comm.). Stems and internodes are shorter than those of related hemiepiphytes.

Orchid monocots. Orchidaceae owe their numerical superiority among epiphytes to an exceptionally propitious set of vegetative and reproductive features and to extraordinary cladogenesis promoted by specialized pollination syndromes (Benzing & Atwood, 1984). Vegetative mechanisms vary tremendously according to the taxon's native substratum and ecoclimatic conditions. But there are several important attributes common to all canopy-dependent family members that, in some form, predisposed early stock for arboreal life. For example,

epiphytic Orchidaceae possess specialized roots varying in photosynthetic performance and water relations, depending on structure and metabolism; uptake is enhanced in all cases by a nonliving velamen which imbibes precipitation and contained solutes for subsequent sorption through transfer cells in an underlying exodermis (Benzing et al., 1983; Benzing & Pridgeon, 1983; Fig. 10). This same mantle effectively retards desiccation injury from both short-term and extreme drought (Benzing, 1986a). Velamina simply embolize air in order to break the hydraulic continuum that, if left intact, would allow matric forces in adjacent drying substrata to dehydrate living epiphyte tissue. A green cortex supplements shoot photosynthesis and is the major site of carbon gain for the plant in exceptional cases (Fig. 4). Hyperovulate gynoecia and aggregated pollen characterize most of the family. Microspermy—up to millions of tiny, lightly provisioned seeds per capsule—requires fungal intervention for germination. High-fidelity, long range, but often inefficient pollinators promote ethological isolation leading to plant speciation (Benzing & Atwood, 1984).

Pre-epiphytic orchid stock probably possessed structurally modified, locally suberized epidermis/hypodermis layers as do most extant terrestrial family members and some other monocots (e.g., *Zea, Allium, Amaryllis*). Similar root specialization is less known in dicots. Microspermy and associated mycotrophic nutrition were probably also acquired in a terrestrial context, as suggested by the current habitats in which all other such heterotrophic plant symbioses occur (e.g., Monotropaceae, achlorophyllous Gentianaceae). Production of numerous tiny diaspores, subsistence on transitory resource supplies, and maintenance of high water and nutrient use efficiencies set the stage for migration to forest canopies, including many uninhabitable by less stress-tolerant epiphytes. Evolution of pheromonelike fragrances and specialized floral morphology tightened relationships with specific hymenopterans and dipterans, and assured extensive proliferation of several clades that happened to be canopy-dependent. Large clusters of related species among taxa relying on smaller, short-range vectors with no known propensity for exclusive foraging suggest that substratum-specific factors have also been important. As in a number of other diverse communities of sessile organisms, coexistence of densely packed epiphyte popula-

tions may be favored on substrata subject to intermediate disturbance (Connell, 1978; Benzing, 1981, 1986b). Radiation in other speciose, canopy-dependent taxa visited by opportunistic or sedentary pollinators (e.g., *Anthurium, Peperomia*) may be due to similar phenomena.

Dicots. Magnoliopsida are, on the whole, poorly disposed to epiphytism—just 2% of species are involved—but there are exceptional taxa (Gentry & Dodson, 1987). Success in a clade is often predicated on a single theme and no other family incorporates the diverse resource procurement mechanisms or stress tolerances exhibited by epiphytic Bromeliaceae and Orchidaceae. Except in Marcgraviaceae, dicot terrestrials always outnumber confamilial epiphytes. In tree crowns, *Peperomia* ranks first in size among successful dicot genera and even families, a statistic fostered by pantropical distribution, the presence of CAM variations (Sipes & Ting, 1985), and high-volume production of small adhesive fruits. Habits range from shrubby to minute and creeping. Moraceae also owe much of their major epiphytic presence to a single genus (*Ficus*) with a similar broad range; here the strangler habit provides the vegetative basis for success. Rampant speciation within a relatively narrow adaptive profile has again been encouraged by circumtropic range and host-specific pollinators—in this case, the fig wasps. According to Ramirez (1977), the moraceous strangling habit evolved "as a response to lack of light at the forest level." Necessary attributes for success included presence of viscid hyaline coats on seeds that would germinate only on moist humus, long aerial roots, water-use-efficient seedlings, and dispersal by winged vertebrates. Marcgraviaceae and Clusiaceae are additional single-strategy families, emphasizing secondary and primary hemiepiphytism respectively. Stranglers also occur in *Schefflera* (Araliaceae), *Posoqueria* (Rubiaceae), *Metrosideros* (Myrtaceae), and elsewhere, but they are atypical among confamilial canopy-based taxa.

Most epiphytic Asclepiadaceae belong to closely related, succulent, vining *Dischidia* and *Hoya*. Flasklike leaves of *D. rafflesiana* and several other species enclose nests; ants provide dispersal service for many more. Forms with less specialized foliage regularly root in or grow against ant debris, providing clues as to how ant-fed relatives evolved. Dome-shaped leaves of *D. collyris* grow tightly pressed against bark, providing

shelter for *Iridomyrmex* colonies (Huxley, 1980). Photosynthesis involves CAM and/or CAM-cycling (Kluge & Ting, 1978). Cactaceae became equipped for the canopy-dependent synusia through drought selection in terrestrial habitats. Fleshy, small-seeded fruits and climbing habit would eventually favor life in canopies. Movement into tree crowns appears to have involved some reversals. Originally aphyllous, stems of the most advanced epiphytic forms (which happen to be natives of humid forests—e.g., *Zygocactus, Ripsalis*) have lost their armature and become much flattened, or narrowed if still terete (e.g., *Hatiora*), presumably to improve performance in shade. Family-wide CAM is probably present in relatively muted form as well. Response to the resulting elevated moisture demands requires uptake by long-lived roots from more or less continuous supplies in tree fissures or soil (the secondary hemiepiphytes). Despite the extreme drought tolerance of many terrestrial relatives (e.g., *Maxillaria, Ferrocactus*), epiphytic Cactaceae seemingly never colonize the most demanding bark and twig exposures.

Less obvious is the basis for high epiphyte success in Ericaceae, Gesneriaceae, Melastomataceae, and nonmyrmecophytic Rubiaceae. Most canopy-dependent members in all four families grow exclusively on humus mats in humid forests. Woody habits and sclerophyllous foliage, sometimes complemented by storage tubers, characterize Ericaceae and Melastomataceae. About one-half of the rubiaceous epiphytes (*Hydnophytum, Myrmecodia*) supplement mineral nutrition and store moisture via ant-inhabited, swollen hypocotyls (Fig. 12). Basically herbaceous Gesneriaceae feature broader growth-form variety, and several genera contain CAM plants. Like some *Peperomia*, these gesneriads exhibit trilayered mesophyll that may signal unusual photosynthesis. Substrata are more diverse in this family, ranging from ant-carton to less specialized humus. *Codonanthe* and related genera, along with some hemiepiphytic cacti, are probably the best drought-insulated of the dicot epiphytes. Baccate fruits provide seed mobility in most cases, although *Rhododendron*, a few gesneriad genera, and large proportions of Melastomataceae and Rubiaceae ripen wind-borne seeds. Ant-associated species are myrmecochorous.

Representation in canopy habitats varies among these families, ranging from 4% to 35% of all genera in Rubiaceae and Ericaceae respectively (Madison, 1977). The ericad statistic is all the more impressive considering the family's size and numerous temperate taxa. The other three families are larger and nearly or exclusively moist-tropical, hence have had greater access to arboreal habitats. Breadth and depth of specialization for canopy dependence is further indicated by comparing the total of exclusively epiphytic genera containing two or more species with the number which include soil-based species as well. Gesneriaceae are most canopy-adapted by this measure with 13 genera meeting each criterion, while Ericaceae is least so with only four terrestrial-free genera out of 22 containing epiphytes; the largest of the four contains only eight species. *Vaccinium* is especially noteworthy for its wide range throughout Old and New World boreal to equatorial zones and diverse habitat assignments. Epiphytic only: mixed genera ratios for Melastomataceae and Rubiaceae are 8 : 12 and 5 : 14.

The influence of geography in determining which families would contribute the most species to the forest canopy flora (Gentry & Dodson, 1987) is apparent in Magnoliopsida. Epiphytic Gesneriaceae are centered in the neotropics where tribe Episcieae and particularly genera like *Drymonia, Columnea, Dalbergaria*, and *Trichantha* have radiated extensively in tree crowns. Speciation here, as in epiphytic Liliopsida (Araceae, Bromeliaceae, Orchidaceae), appears to involve specialized American pollinators (hummingbirds and euglossines). Paleotropical counterparts are far fewer but still number more than 100 species. Canopy-dependent ericads are also disproportionately neotropical and ornithophilous. All but a small fraction of the peperomias are American, although little is known about the group's reproductive biology. Because 73% of Costa Rica's large fern flora roots in tree crowns (Wagner & Gómez, 1983), it appears that neotropical epiphytism is not all pollinator-related. Wide availability of moist montane forest in the northern Andes and Central America, which is reputedly amenable to fine niche partitionment (Gentry & Dodson, 1987), has also been important for expansion of American forms. Melastomataceae and Rubiaceae number among the few heavily epiphytic pantropical families that failed to generate more New than Old World epiphytes. Scrutiny of reproductive systems and pertinent vegetative characters might help ex-

plain why mechanically-dependent New World portions of these two families have failed to undergo as much cladogenesis as have many co-occurring epiphytic pteridophytic and angiospermous groups.

Chemical peculiarities of substrata or unusual mycorrhizae may be responsible for uneven epiphyte development among higher monocot and dicot taxa. Ericaceae, Melastomataceae, and Orchidaceae exhibit family-wide affinity for acidic, often humid and organic, infertile soils. Little is known about the physiochemical details of canopy surfaces, but available nutrient ions are probably often scarce. Substrata in everwet forest where most epiphytes live tend to be sodden, at least moderately acid, and certainly organic. Use of NH_4^+ rather than oxidized nitrogen by plants native to such substrata may have been a predisposing character for epiphytism. Ericads are notably deficient in nitrogen reductase, a sign of long dependence on reduced nitrogen. Ericaceae were perhaps especially well positioned for canopy invasion through formation of mycorrhizae of a type seen in some extant terrestrials that mobilize nitrogen and phosphorus from sterile, organic soil (Stribley & Read, 1975; St. John et al., 1985). Terrestrial Orchidaceae are also strongly mycorrhizal, but the advantages, if any, that fungi provide canopy-dependent adults remain little studied and controversial (Hadley & Williamson, 1972; Sanford, 1974; Benzing & Friedman, 1981). Broad surveys of epiphyte roots and nitrogen-cycle microbes in canopy substrata could prove rewarding. A general work-up of tree-crown media as nutrient sources is much needed.

Mistletoes. Restricted taxonomic participation in branch parasitism is made all the more intriguing by the widespread abundance of mistletoes, some of which range farther north than any vascular epiphyte. Virtually the entire complement—about 1,300 species—belongs to Santalales. Why many thousands of plants from so many other higher taxa root nowhere but on bark yet never invade host vasculature is puzzling. Occurrence in Santalales of terrestrials with haustoria, including primitive Loranthaceae, but no epiphytes suggests that branch parasitism arose from root parasitism. Perhaps more direct aerial transitions were precluded by biomechanical constraints. Mistletoes transpire profusely even during drought in order to acquire sufficient nitrogen from host xylem (Ehleringer et al., 1985). This is the antithesis of an epiphyte's usual conservative water use pattern. Failure by so many

epiphytic lineages to achieve parasite status simply because invasive organs are difficult to acquire seems unlikely in light of the diverse soil-based species that tap any nearby roots. More plausible is the theory that continuous function during a historical crossover between the high solute potential/low maximum turgor/sensitive stomata pattern of the epiphyte and the three to five times more concentrated osmotica (Harris & Lawrence, 1916; Harris, 1918) and correlated foliar conductance patterns of the parasite would require buffering, which is less available in canopy than in terrestrial habitats. Most of the root hemiparasite's absorptive apparatus continues to function in the conventional manner, drawing upon soil moisture and thus reducing the liability to water loss of transitional forms.

SUMMARY

Epiphytes do not constitute a narrowly defined group of plants on either taxonomic or functional grounds, nor is their habitat usually unique in its important physical characteristics. Growing conditions in both humid and arid forest canopies overlap with those at ground level, as do adaptive mechanisms in canopy- and soil-dependent flora. Substrata exhibiting the most unique and powerful constraints on plant success occur in the driest exposures. Circumvention of dependence on soil by epiphytes is varied. Modes of moisture and nutrient acquisition are the most unusual, especially among PS forms. Ways in which resources are conserved and deployed are often variations on, and perhaps sometimes identical to, patterns present in terrestrial relatives. No single key feature—like CAM, impoundment habit, or animal dispersal—nor combination of key characters underlies epiphytism. Solutions are many, a condition favoring broad taxonomic composition of mechanically-dependent synusiae. In contrast, failure of a large tropical group to evolve epiphytic members may relate to the presence of a few well-entrenched, maladaptive features. Evolutionary inertia probably also reflects little-understood genetic constraints and functional incompatibilities that block emergence of enabling syndromes even though some of their mechanistic components are already well established.

Cladogenesis and adaptive radiation for life on varied substrata have been more closely allied in some epiphytic taxa than in others. Most families, even some containing hundreds of epi-

phytic species, have entered forest canopies through a single vegetative theme. Propitious relationships with pollinators, intermediate disturbance, and narrowly circumscribed substratum requirements are among the agencies that have promoted astounding speciation in several heavily canopy-dependent taxa. Speciation sometimes required no accompanying displacement of nonfloral characters. Bromeliaceae and Orchidaceae are exceptional for their diverse vegetative mechanisms. These two families do well under equable conditions, but they are especially dominant in stressful environments because they can maintain enough generative power to compensate for mortality imposed by habitat patchiness and disturbance.

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